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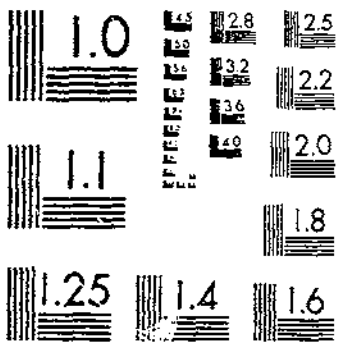

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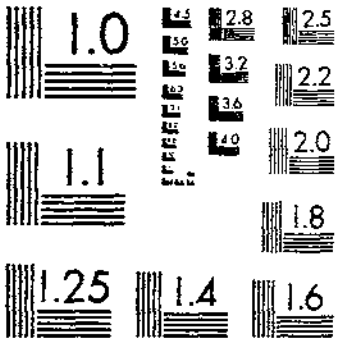

MICROCOPY RESOLUTION TEST CHART
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GONIOZUS GALLICOLA FOUTS, A PARASITE OF MOTH LARVAE, WITH NOTES ON OTHER BETHYLIDS (HYMENOPTERA: BETHYLIDAE; LEPIDOPTERA: GELECHIIDAE)

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Washington, D.C. Issued February 1976

GONIOZUS GALLICOLA FOUTS, A PARASITE OF MOTH LARVAE, WITH NOTES ON OTHER BETHYLIDS (HYMENOPTERA: BETHYLIDAE; LEPIDOPTERA: GELECHIIDAE)

By GORDON GORDH, *Systematic Entomology Laboratory, Northeastern Region, Agricultural Research Service*

The Bethyloidea, a comparatively small superfamily, are considered the most primitive of extant aculeate Hymenoptera (Malyshev *1968*).[1] The cosmopolitan Bethylidae occupy a central position in this superfamily, with approximately 300 Nearctic species north of Mexico (Evans and Eberhard *1970*). All species for which biological information is available are parasitic. Behaviorally the bethylids appear transitional between the nonaculeate Chalcidoidea and the more advanced aculeates. Numerous studies on these wasps have suggested diverse behavioral adaptations and host affinities (Back *1940*; Bridwell *1917*, *1918*, *1919*; Busck *1917*; Cherian and Israel *1942*; Hyslop *1916*; Iwata *1949*, *1961*; Kearns *1934*; Sauer *1938*; Schaefer *1962*; Willard *1927*). However, only a few extensive examinations have been conducted on the bethylids (Finlayson *1950a*, *b*; Rilett *1949*; van Emden *1931*; Voukassovitch *1924*; Yamada *1955*). Most of these studies have centered primarily on beetle parasites, which are distantly related to the Bethylinae. Since *Goniozus* consists exclusively of lepidopterous parasites, a critical examination of *Goniozus gallicola* is desirable to know more about the behavior of the Bethylinae.

G. gallicola (fig. 1) was described from Oregon by Fouts (*1942*). Although the parasite was not reared, Fouts indicated it was probably a parasite of *Melissopus* sp. on oak. No subsequent host association of the parasite has been recorded.

[1] The year in italic after the author's name indicates the reference in Literature Cited, p. 23.

The field-collected host of *G. gallicola* is *Deoclona yuccasella* Busck. Details of the life history of this moth are fragmentary. Described in 1903 from specimens taken near Los Angeles by Albert Koebele, *D. yuccasella* has been largely ignored by plant ecologists and lepidopterists alike. The only known plant host of *D. yuccasella* is *Yucca whipplei* Torrey. Powell and Mackie (*1966*) reported that the moth is presumably diurnal, but I have not confirmed this. For a description of the immatures, see Keifer (*1936*).

During the winter *D. yuccasella* may be collected in southern California feeding on dry seeds in dehiscent pods, and several instars can be recovered from any given population. The larva gradually creates a cavity between seeds. If seed tiers containing the larva are deliberately split, exposing it, it immediately begins to seal the opening with silk. For a review of the moth's distribution and activity, see Powell and Mackie (*1966*).

Numerous insect associates of *Y. whipplei* have been reported, but apparently only one pollinator, *Tegeticula maculata* (Riley), exists. Three allopatric forms of the pollinator have been recorded (Powell and Mackie *1966*). The pollinator is absolutely dependent on *Y. whipplei* for development, and the plant has no other known means of pollination. The moth larva feeds on developing *Yucca* seeds, but it pupates in the soil. For a résumé of the pollinator's life history, see Powell and Mackie (*1966*) and Wimber.[2]

In addition to the pollinator, *Y. whipplei* harbors several insect species that are totally dependent on the plant for nutrition and a pupation site. Three species of *Prodoxus* (Lepidoptera: Incurvariidae) have spatially subdivided and live in the plant: *P. aenescens* Riley in the apical stalk region, *P. marginatus* Riley in the petioles and pods, and *P. cinereus* Riley in the basal part of the stalk. Powell and Mackie (*1966*) also recorded the blasobastid *Holcocera gigantella* Chambers from San Diego County, Calif., but I have not recovered this moth from Riverside and San Bernardino Counties in this State.

Of the four species of *Yucca* growing in California, *Y. whipplei* is unique in having its own pollinator, possessing closed stigmatic ducts, and being the only member of the subgenus *Hesperoyucca*. In California *Y. whipplei* is cismontane, distributed from Monterey County southward and along the Tehachapi Mountains

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[2] WIMBER, D. R. POLLINATION OF YUCCA WHIPPLEI TORR. [Unpublished master's thesis. Copy on file Grad. Sch., Claremont, Calif.] 1958.

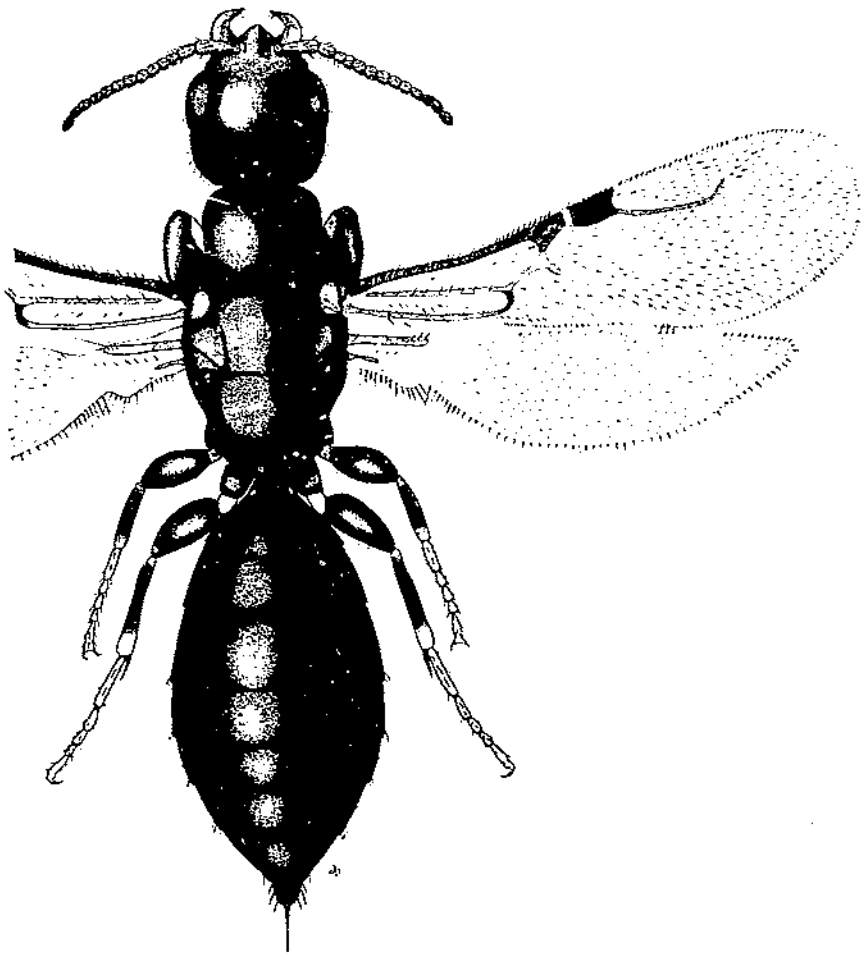

FIGURE 1.—*Goniozus gallicola* female, dorsal aspect.

(Jepson *1925*). In southern California it is found in xeric habitats and desert areas. For an extensive treatment of its distribution, see McKelvey (*1947*).

Peculiarly *Y. whipplei* dies after producing only one fruiting stalk. McKelvey (*1947*) indicated that individual rosettes require 6–7 years to mature. Powell and Mackie (*1966*) noted that fruiting scapes develop during the spring, and this is consistent with my observations. They also reported that the bloom of *Y. whipplei* lasts 15–24 days and pod development 53–87 days. Upon seed maturation, pods split open, and the discharged seeds are dis-

persed by wind and birds. Plants are solitary in southern California, although they are apparently caespitose in the northern area of their distribution. This high degree of variability in growth habit prompted Haines (*1941*) to erect five subspecies for *Y. whipplei*.

MATERIALS AND METHODS

Adults of *G. gallicola* were reared from parasitized *D. yuccasella* larvae that developed in *Y. whipplei* seed pods collected 8 miles south of Sun City, Riverside County, during November 1972. Female parasites were isolated in cotton-plugged 4-dram glass vials with honey streaks as a nutrition source. Hosts were provided for each bethylid, and oviposition was observed daily. Parasitized hosts were removed from vials and placed in petri dishes, where parasitic development was observed.

Host material was collected from *Y. whipplei* at four localities in San Bernardino and Riverside Counties throughout the winter, and seed pods were stored at 10° C until needed. This procedure did not affect host survival but did retard development and preclude emergence of field-collected parasites included with the plant material.

When the *G. gallicola* culture was sufficiently large, 50 newly emerged mated females were individually placed in numbered snap-cap, plastic, 2-dram vials with honey streaks applied to the inner surface of each lid. One host was placed with each female parasite. The following observations were made daily: (1) Whether the host was paralyzed and parasitized and, if so, (2) host size, (3) number and position of parasite eggs, and (4) extent of host feeding. This information was collected throughout each female parasite's lifetime. Parasitized hosts were individually placed in No. 1 gelatin capsules, and the capsules were sequentially taped to cards bearing the vial number of the appropriate female parasite. Thus, changes in progeny development time, sex ratio, and immature mortality were noted, and this information was correlated with the female parasite's age. During the study nine parasites were accidentally killed or escaped during host transfer.

Hosts and parasites used in some behavioral studies were handled slightly differently. To maintain a supply of paralyzed host larvae, hosts were placed with newly emerged parasites in a petri dish for several hours. Periodic observations were made for

paralyzed larvae. These were removed and placed in a series of plastic vials, with no more than five per vial. Paralyzed hosts were discarded if not used within 10 days.

To aid future workers in biological and systematic studies of this parasite, voucher specimens of *G. gallicola* have been distributed to the following institutions or individuals: Entomological Museum, University of California, Riverside; California Academy of Science, San Francisco; J. Powell, University of California, Berkeley; Canadian National Collection, Ottawa; H. E. Evans, Colorado State University, Fort Collins; Snow Entomological Museum, University of Kansas, Lawrence; British Museum of Natural History, London; Soviet Academy of Science, Leningrad; Plant Protection Research Institute, Pretoria, South Africa; Ehime University, Matsumaya, Japan; and U.S. National Museum of Natural History, Washington.

RESULTS

Stages of Development

The egg of *G. gallicola* (fig. 2, *A*) is hymenopteriform, slightly curved, nearly translucent, without sculpture, and it measures approximately 0.8 mm long and 0.2 mm in diameter. Each egg is firmly attached to the host's integument and deposited parallel to the longitudinal axis of the body. Several eggs may be deposited per segment, with definite site preference exhibited by the female parasite. During oviposition the sting is exserted and its ventral surface used to press the egg firmly to the host. Deposition of an egg requires 1.5–4.0 minutes.

Orientation of the egg is precise, but the direction of the female's ovipositional stance is not. The region of the chorion beneath which the parasite's mouth parts develop always adheres to the host's cuticle, but larval development may be directed anterior or posterior to the host's longitudinal body axis.

Hatching occurs 24–36 hours after egg deposition. The exact time of eclosion is exceedingly difficult to determine, since virtually no external change occurs. Once the egg hatches, the position of the larva remains fixed. The nearly translucent first-instar larva is apodous, lacks any sign of external segmentation, and may be distinguished from the egg only by spasmodic waves of gut contraction and the movement of host hemolymph within the parasite's body. Older first-instar larvae (fig. 2, *B*) exhibit a

slight, but distinct, transverse cephalic constriction, and the posterior end becomes enlarged. Later stages may be recognized by the development of conspicuous tracheae.

The larval head of *G. gallicola* does not project through the host integument. Instead, the larva appears to attach itself in a suckerlike fashion, with the mandibles firmly embedded in the host cuticle. Pulling the parasite larva from the host is difficult and invariably results in the parasite's death. During the parasite's first instar the host is alive, or at least probing with an insect pin elicits writhing.

Feeding by the parasite requires 3–4 days ($\bar{x}=3.6\pm0.5$, $n=84$) and is temperature dependent. The number of parasite larvae per host and the host body size have some effect on the rate of feeding, but they were not statistically significant in this study. Parasite larvae usually exsanguinate the host, and upon completion of feeding the host consists of a shriveled integument and cranial capsule.

If the parasite prepupal stage is defined as the period between the cessation of feeding and the transformation into the pupal form, the duration of this stage is 3–5 days ($\bar{x}=4.1\pm0.7$, $n=84$) and is also temperature dependent. Superficially the prepupa resembles the feeding larva (fig. 2, *C*) except the cuticle is opaque and the spherules or urate cells are distinctly white.

The cocoon of *G. gallicola* is loosely woven, white, 5 mm long, and 1.5 mm in diameter. Its construction requires 14–20 hours at 25° C. After the cocoon is completed, a dark-red fluid is secreted from the posterior tip of the gaster. This fluid hardens within several minutes depending on the ambient humidity. Voiding of the hindgut may be stimulated prematurely if the spinning larva is probed with a dissecting needle. In all instances the fluid is voided in less than 15 seconds.

Upon assuming the pupal shape, the parasite's body is completely white with translucent appendages. Pigmentation occurs in a characteristic fashion (fig. 3) and is similar in both sexes. Initially the posterior margin of each compound eye is pink (fig. 3, *A*). As the coloration darkens, the entire eye becomes brown. Darkening occurs during the first day after the pupal shape is assumed. Concomitantly the ocelli become pink then dark red. Next the mesoscutum, scutellum, mesepisternum, mesepimeron, and lateral margins of the propodeum become dusky. As these regions progressively darken, the head becomes

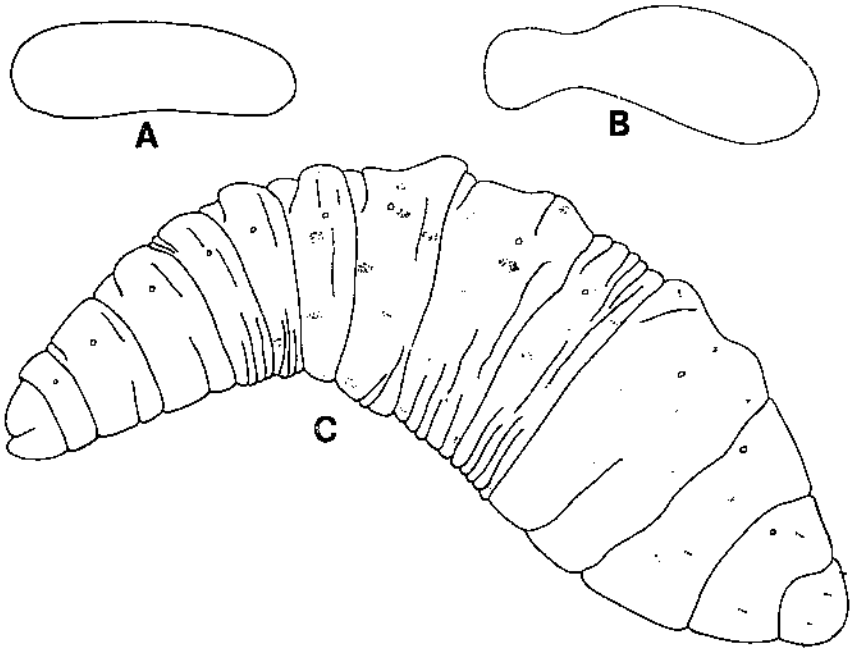

FIGURE 2.—*Goniozus gallicola: A*, Egg; *B*, larva; *C*, prepupa.

dusky along the posterior margin. The coloration darkens as it sweeps anteriorly toward the mandibles (fig. 3, *B* and *E*).

The mesosoma is nearly coal black before the gaster shows any noticeable coloration. The posterolateral margins of tergites I–V become dusky, and the first tergite quickly becomes concolorous with the mesosoma. Darkening on the tergites proceeds mesally along the posterior margin (fig. 3, *B*) until a continuous band is produced. A similar pattern is developed for sternites I–V (fig. 3, *E*). When each color band is continuous, a general darkening of each segment occurs. However, the most posterior gastral segments do not appear to follow this pattern. Instead, they remain light until the other segments become darker, and then they become progressively and uniformly darker except the gonopods, which remain light until just before adult emergence (fig. 3, *F*).

Appendages remain translucent except the coxal coloration, which occurs simultaneously with the mesosomal darkening. The femora and tibiae darken concomitantly with gastral sternites I–V. Immediately prior to adult emergence the parasite's antennae and tarsi become honey colored.

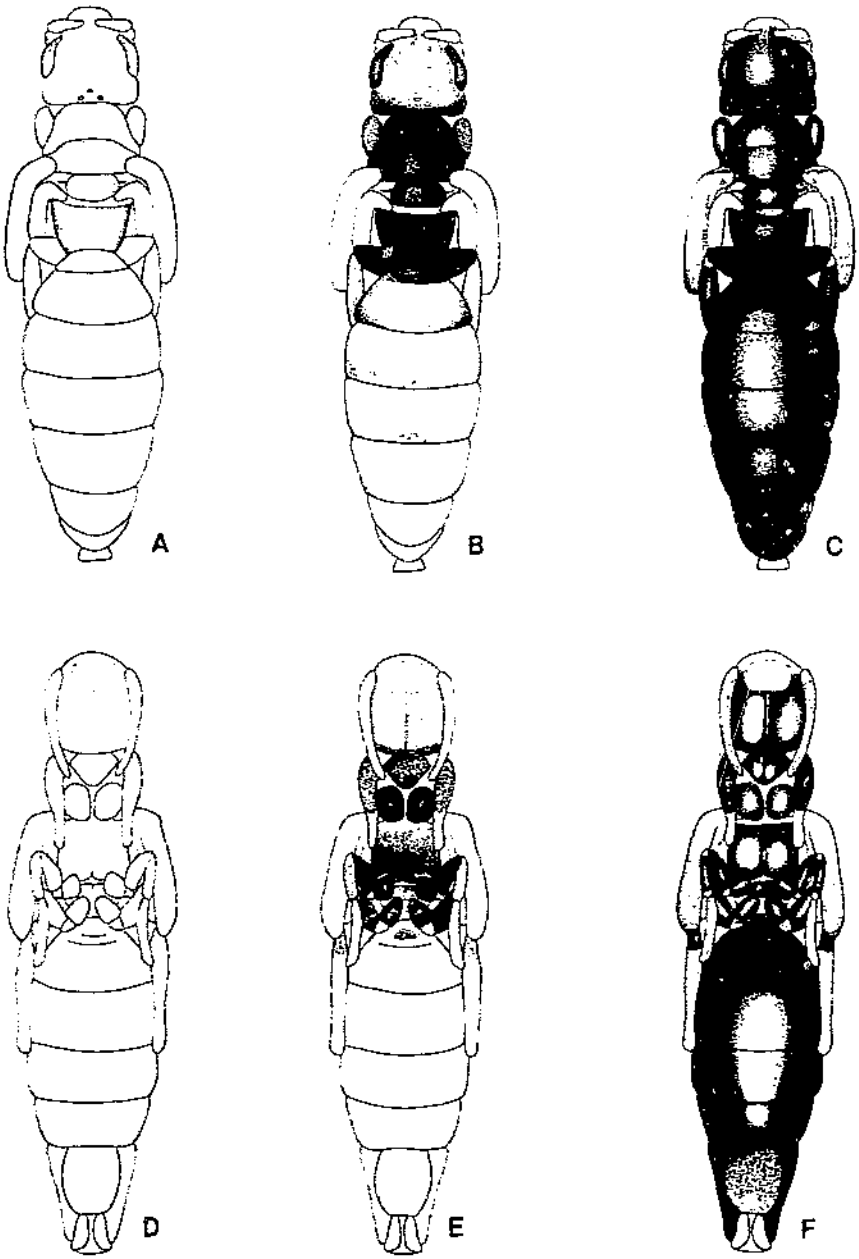

FIGURE 8.—Pupal pigmentation in *Goniozus gallicola*: *A-C*, Female, dorsal aspect; *D-F*, male, ventral aspect.

Mating and Sex Ratio

G. gallicola is protandrous, with males emerging up to 10 hours before sibling females. After emergence, males exhibit no tendency to leave the pupation site but instead begin to chew holes in female cocoons. No specific site is selected; the male may choose the anterior or posterior end of a female's cocoon. Once inside the cocoon, the male orients toward the female, head to head and venter to venter. There appears to be little or no courtship behavior, and copulation requires 4–18 minutes. After completing insemination, the male leaves the cocoon and repeats the procedure with another female. It is unknown precisely how a male perceives a female's cocoon, but since broods are strongly spanadrous, perception of a female inhabitant may not be mediated through a chemical messenger, i.e., sex pheromone. After mating with several females, the male will often move about the container and feed on honey. Mating may also occur after female emergence.

Twenty-five-day-old parasites of both sexes that had been isolated as pupae in 2-dram vials with honey streaks were observed to mate readily. Mating behavior of emerged virgins involves little courtship behavior: Receptive females remain motionless with antennae rigidly at right angles to the longitudinal axis of the body and parallel to the substrate. The male usually approaches from the side or rear, mounts, places his foretarsi on the lateral margin of each folded female wing, puts his middle tarsi along the distal margin of each wing, and crosses the hindtarsi around the female's seventh gastral sternum. Duration of copulation is variable, requiring 30 seconds to 4 minutes. In several instances males discontinued copulatory attempts, dismounted, and groomed themselves. The females then remained motionless with antennae perpendicular to the body and parallel to the substrate. Mated females repel subsequent male advances. If a male succeeds in mounting an unreceptive female, she runs rapidly about the container. If this behavior does not dislodge the male, she stops and writhes. Often females were observed attempting to sting males during dislodgment.

The sperm of 25-day-old males is apparently viable, since inseminated females allowed to paralyze and parasitize hosts produced female offspring. Two females that had produced several female-biased broods began to produce only males, and it was assumed they had depleted their sperm supply. Although alternative hypotheses seem plausible (i.e., some physiological disturbance or mechanical damage), it is nevertheless interesting to

note that these females accepted males and successfully copulated. One of the second-mated females was subsequently killed by a host larva, but the other produced females on her last two hosts.

To determine the sex ratio of *G. gallicola*, 10 mated females were isolated in the previously described manner. Their parasitized hosts were placed in sequentially numbered gelatin capsules. The number of eggs deposited, position, host size, number of adults recovered, and sex ratio of each brood were recorded and the data tabulated for each female's lifetime. These females parasitized a mean of 27.27 ± 6.84 hosts and deposited 1,724 eggs.

G. gallicola apparently can regulate its sex ratio according to host size or number of eggs laid per session or both. Table 1 is a chi-square goodness-of-fit test with 100 randomly selected broods. Studies suggested that in a small brood with approximately 10 parasites, only 1 male was produced, but larger broods

TABLE 1.—χ^2 *goodness-of-fit test of* Goniozus gallicola *sex ratio on* Deoclona yuccasella

[Extrinsic hypothesis: 1 male per brood]

Brood size	Hypothesized ratio	Total broods	*F* (expected)	*F* (observed)	χ^2 [1]
1	1:0	8	8	10	0.50
2	1:1	13	13	14	.08
3	1:2	22	22	24	.18
4	1:3	17	17	20	.53
5	1:4	16	16	21	1.50
6	1:5	15	15	17	.27
7	1:6	13	13	15	.31
8	1:7	8	8	10	.50
9	1:8	15	15	21	2.40
10	1:9	3	3	4	.33
Total	—	130	130	156	6.60 n.s.
11	1:10	5	5	10	5.00
12	1:11	2	2	5	4.50
13	1:12	1	1	5	16.00
14	1:13	1	1	6	25.00
15	1:14	1	1	3	4.00
Total	—	10	10	29	54.50***

[1] χ^2 8(0.05)=15.51; χ^2 8(0.1)=13.36; χ^2 3(0.05)=5.99; χ^2 3(0.005)=12.84.
n.s. = not significant.
*** = significant at 0.005-percent level.

produced more than 1 male. This analysis suggests that the sex ratio fluctuates with increasing number of eggs deposited.

Emergence of recently mated female siblings was often observed to be synchronous. Stimuli responsible for the synchrony were not determined, but presumably changes in light intensity and temperature as well as container movement were responsible rather than an endogenous rhythm.

Parasite Attack and Oviposition

G. gallicola has a 2- or 3-day preoviposition period, during which hosts are frequently stung, but eggs were not observed to be deposited. Parasite attack is rather specific. The female attaches to the host's cuticle and embeds her mandibles in the host's dorsum immediately behind the head capsule. She then thrusts her gaster forward and injects venom near the host's ventral nerve cord just posterior to the gula. Several observations were made of females that failed to attach in this manner. Two alternatives were observed of such misdirected attacks: Either the parasite would quickly shift its position to the head and direct its sting to the appropriate locality, or the host larva would kill the parasite by decapitation with its mandibles.

Paralysis of *D. yuccasella* requires 2 or 3 minutes, during which the parasite waits 5 or 6 cm away grooming itself. Venom of *G. gallicola* appears localized in its effectiveness but produces complete paralysis. Senescent female parasites 50–60 days old twice were observed attached to the intended host at a position not suitable for injecting venom at the appropriate site. Each time the parasite was attached close enough to the host's head so that the larva's mandibles could not reach it. Both times the female parasite repeatedly thrust the sting into the host's body, presumably injecting venom with each stab. Each episode lasted 10–15 minutes, but paralysis was not observed.

Paralyzed host larvae are incapable of locomotion, but still they respond to tactile stimulation. Those removed prior to oviposition by female parasites remained responsive to probing for 10–12 days. Laboratory hosts such as *Pectinophora gossypiella* (Saunders) and *Phthorimaea operculella* (Zeller) readily pupate if they have been stung near the time of pupation. Eggs deposited on such hosts never develop.

Eggs may be deposited on the host within an hour after paralysis, or the parasite may wait up to 6 days before laying eggs. Female parasites will frequently host-feed before oviposition, but male parasites have not been observed feeding on hosts.

Oviposition may last several hours. Occasionally during egg deposition a female parasite may become quiescent or leave the host for several minutes but invariably returns to deposit more eggs. Once a full complement of eggs has been laid, the female will leave the host and move about the container. She does not show interest in the parasitized host and does not eat her own young.

The parasite prefers to lay eggs on the host's dorsum, especially on segments 6–9. Figure 4 shows the number of eggs deposited and cumulative percentage for each body segment based on data collected from 205 randomly selected parasitized larvae of *D. yuccasella*. Although eggs were not observed on segments 2, 13, and 14, this seems to be an artifact of host paralysis. These segments were contracted on paralyzed larvae, and consequently the surface area available for the reception of eggs was considerably reduced. Egg distribution as a consequence of experimental design seems unlikely, since hosts were oriented in several ways between *Yucca* seeds when offered to female parasites. Moreover, inverting paralyzed larvae and wedging the dorsum in a groove elicited the same response: Parasites would work their bodies between the substrate and the host dorsum and oviposit on the host's back. Presumably selective pressure has so operated on the parasite that dorsal oviposition is favored.

Paralyzed larvae are capable of spasmodic movement but not locomotion. Body contraction is from side to side or head to caudal end, with the ventral part of the segments contracted. Any movement of the host increases the possibility that a parasite's

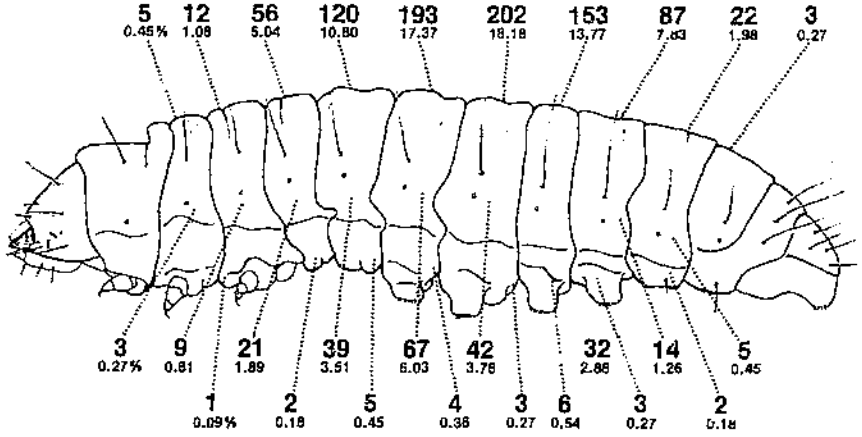

FIGURE 4.—Semidiagram of *Deoclona yuccasella*, host of *Goniozus gallicolla*, showing number of parasite eggs deposited and cumulative percentage.

eggs will be damaged or dislodged. The parasite egg chorion is comparatively thin and easily damaged. Also, movement of the eggs on the host cuticle reduces the possibility of successful parasite development. Since parasite larvae are apodous, they attach only with the mandibles. Any host movement that would cause dislodgment increases the probability of parasite death.

Host paralysis by a particular parasite is not an essential prerequisite for her oviposition. Hosts that were paralyzed by female parasites, removed before oviposition, and then offered to another female often elicited an ovipositional response from the second parasite without parasite stinging. In a related experiment when paralyzed and parasitized hosts were exposed to a second nulliparous parasite, it exhibited ovipositional restraint. When eggs were removed from the integument and the paralyzed host was offered to a nulliparous female, a second clutch of eggs was deposited. This suggests that a chemical, which might serve as a spoor (Flanders *1951*) or a kairomone (Brown et al. *1970*), is not deposited on the host's body.

G. gallicola apparently responds to the size of its host and deposits more eggs per clutch on larger hosts provided it has been mated. This relationship does not hold if it is unmated. Figure 5 shows the number of eggs deposited on hosts of different

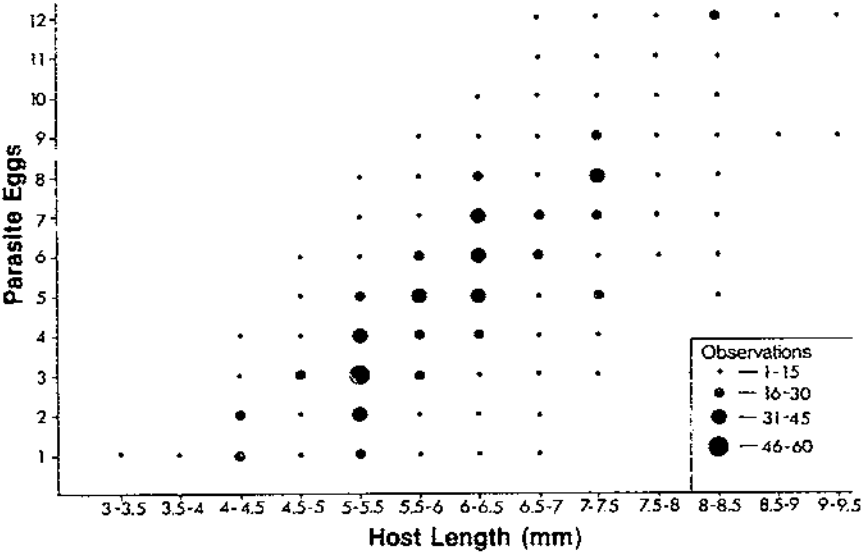

FIGURE 5.—Scattergram of number of *Goniozus gallicola* eggs deposited and length of *Deoclona yuccasella* host.

size (n=873). Experiments to determine the significance of this phenomenon were inconclusive. An attempt was made to transfer larvae from one host to another and thereby create superparasitism. However, manipulated larvae invariably failed to attach to the new host and died. When parasite broods were reduced in size, development time of the remaining immatures and size of the emerging adults were not significantly different from those of control broods.

The mean longevity of mated *G. gallicola* females having access to hosts was 62.43±8.48 days (n=41). They deposited 153.78± 48.59 eggs. Mated females fed honey but deprived of hosts throughout their lives lived 71.02±6.1 days (n=50). The difference seems due to the parasites' frequent loss of legs, wings, or antennae while subduing hosts. Presumably the loss of appendages resulted in reduced longevity. Parasites missing appendages still attempted to paralyze fresh hosts, and when offered subdued hosts, they oviposited on them. Unmated males and unmated females that were provided honey but deprived of hosts lived as long as females provided hosts. Males that mated with several females died in less than 8 days after emergence.

The oviposition behavior of unmated females was tested and compared with that of mated females. Eight virgin females were placed singly in 2-dram vials and provided a single host as previously described. The period between successive ovipositions was longer, but not significantly so. The positioning of eggs and method of host attack were identical in the virgin and the mated females. All eggs developed into males. This suggests that mating is not a stimulus for oviposition and that *G. gallicola* is arrhenotokous.

Host Relationships

The parasite is not host specific, since larvae of *Pectinophora gossypiella* and *Phthorimaea operculella* are also parasitized. Mature *P. gossypiella* larvae are larger than the other host species tested, and more host-induced parasite mortality was observed: 11 of 20 female parasites provided the final instar of this species were killed by the intended host during the first 15 days of parasite life or by the fifth host offered the parasites. The parasite's venom is apparently rather effective on this host because no recovery was observed. This contrasts sharply with the results obtained with an Ethiopian species of *Goniozus*, imported as a potential biological control agent for *P. gossypiella*. This parasite readily attacks *P. gossypiella*, but recovery of numerous hosts has been observed.

The features of larval development on *P. gossypiella* are essentially the same as on the field-collected host *Deoclona yuccasella*. Duration of egg, larval, and pupal periods and adult size were not significantly different between the host species. *Ph. operculella* was also readily attacked by *G. gallicola*. The host struggle is far more vigorous than shown by either *P. gossypiella* or *D. yuccasella*. However, the parasite is still successful in paralyzing *Ph. operculella* but seldom parasitizes it. Paralyzed larvae of this species often turn black and decompose within a few days.

Tests to determine the instar preference of the parasite for *P. gossypiella* and *D. yuccasella* were inconclusive. When simultaneously offered the last two instars of each species, individual parasites would sting all larvae and, if left undisturbed, would oviposit on each paralyzed host. When mature *P. gossypiella* larvae were tested, several paralyzed larvae pupated. Eggs deposited on such hosts were invariably destroyed.

Immature scarabaeid beetles were also offered to the parasite, but all these "hosts" were rejected. Field studies revealed that *Megatoma* sp. nr. *prolixa* Beal is found in association with seed pods of *Yucca schidigera* Roezl ex Ortgies and *Y. whipplei* in southern California, but *Goniozus* has not been observed parasitizing this dermestid. In laboratory studies with *Trichoplusia ni* (Hübner), it was not possible to induce a parasite attack of this species. The last two larval instars were offered to *G. gallicola*, but the host was always rejected.

If more than one parasite is present with a single host, only one female will parasitize it. Sometimes aggressive behavior between parasites was noted when the female parasite on the paralyzed host defended the host and drove off the other parasite.

OTHER BETHYLIDS

Systematic Placement

Bridwell (*1920*) placed bethylids in the following three groups based on host preference and oviposition behavior: *Goniozus* group, which attacks Lepidoptera; *Scleroderma* group, which attacks Coleoptera; and transitional *Epyris* group, which attacks Coleoptera but lays a single egg per host and exhibits fossorial tendencies. Although this system is informative from a comparative ethological standpoint, it has not been followed by contemporary systematists (cf. Evans *1964*; Richards *1939*).

The Bethylinae currently consist of five genera in the Americas—*Bethylus*, *Goniozus*, *Lytopsenella*, *Parasierola*, and *Pro-*

sierola—and less than 100 species (Evans *1964*). Behaviorally and morphologically the Bethylinae are a cohesive group of lepidopterous larval parasites. Nothing is known of the enigmatic South American *Lytopsenella*, although it, too, is presumably a parasite of Lepidoptera larvae. Morphologically *Goniozus* is most nearly related to *Parasierola* (*Perisierola* auct.), but it is separated from that genus on the basis of a few tenuous wing characters. Evans (1964, pers. commun.) suggested that perhaps the two genera may eventually be synonymized after complete taxonomic revision. Behaviorally the genera overlap in several characters.

Bethylids superficially appear relatively featureless as a group, although no extensive treatment of larval morphology has been attempted. The time required for each stage seems to vary little among species. Most studies of bethylids have been conducted under a wide variety of environmental conditions, and sometimes temperature variations have not been reported. Temperature presumably exerts a considerable effect on regulating development time (see Voukassovitch *1924*).

Most bethylids are arrhenotokous, although Keeler (*1939a, b*) reported that a virgin female *Scleroderma immigrans* Bridwell produced female progeny, and Busck (*1917*) noted thelytoky in *Perisierola emigrata* Rohwer. Keeler's findings contradicted those of Bridwell (*1929*) for the same species. Clausen (*1940*) suggested the existence of two races of *S. immigrans*. A culture of a bethylid identified as *P. emigrata* at Riverside, Calif., collected from Hawaii and imported to control *Pectinophora gossypiella*, is clearly arrhenotokous. Thus, in at least two instances the possibility of sibling species in the Bethylidae cannot be overlooked.

Egg Features

In *Goniozus* and *Parasierola* the eggs differ in size and form. Those of *G. claripennis* Foerster are 0.45 mm long, 0.13 mm in diameter, hymenopteriform, but not curved (Voukassovitch *1924*). *G. marasmi* Kurian deposits an egg less than 0.4 mm long, and the egg of *Goniozus* sp. from Ethiopia is less than 0.5 mm long. Eggs of *Parasierola* are consistently larger. Those of *P. cellularis* var. *punctaticeps* (Kieffer) are 0.68 mm long and 0.22 mm in diameter (Nickels et al. *1950*). *P. nephantidis* Muesebeck eggs are 0.75 mm long (Ramachandra Rao and Cherian *1928*). Eggs of *Parasierola* sp. from India average 0.85 by 0.25 mm (Avasthy and Chaudhary *1966*). Those of *Parasierola* sp. from

Colombia are nearly 0.7 mm long (unpub.). The form and exceptionally large eggs of *G. gallicola* suggest they clearly resemble *Parasierola* eggs.

The purpose of the observed transition in egg size between two very closely related genera is uncertain. Iwata and Sakagami (*1966*) suggested egg size may be related to degree of sociality in some bee genera. Since these bethylids are not social, although some species may exhibit social tendencies (sensu Michener *1969*), such an explanation seems unlikely. In all species of *Goniozus* except *gallicola*, the eggs are deposited transversely between segments, whereas *Parasierola* lays eggs longitudinally on host body segments. Ostensibly eggs should be small if deposited between segments and thereby reduce the possibility of damage should the host convulse.

Oviposition

The number of eggs deposited on a host by bethylids varies greatly. Members of such genera as *Holepyris*, *Pristocera*, and *Epyris* only deposit one egg per host, whereas most other bethylids deposit several eggs on each host. Some investigations suggested that several species of *Goniozus* and *Parasierola* can estimate host size and deposit a predictable number of eggs on a given host. Such findings have been reported by Yamada (*1955*) for *G. claripennis* and Kishitani (*1961*) for *G. japonicus* Ashmead. Kishitani (*1961*) demonstrated that *G. japonicus* regulated the number of eggs deposited depending on the size of the available host. However, in contrast to the present study, Kishitani measured head-capsule width and body length of the host and concluded head width affected clutch size. Reaction to host size may be widespread in the Bethylidae, although different physical factors may affect the behavioral response.

Iwata (*1949*) noted that *G. japonicus*, when parasitizing *Dichocrocis chlorophanta* Butler, deposits eggs transversely along the middle dorsum of the host's body. In an extensive study van Emden (*1931*) demonstrated that *Cephalonomia quadridentata* Duchaussoy deposits eggs on ventral intersegmental folds of *Stegobium paniceum* (Linnaeus) larvae and on the abdominal dorsum of beetle pupae. Eggs deposited on the host larval venter have the micropyle attached to the intersegmental fold at the junction of the sternite and pleural region. Gifford (*1965*) reported that *G. indicus* Muesebeck prepares the lateral body section of its host, *Diatraea saccharalis* (Fabricius), with the mandibles before depositing its eggs between segments. *Goniozus* sp.

from Ethiopia deposits its eggs exclusively in the intersegmental folds along the lateral aspect of the host. More than one egg may be deposited per segment in tandem in each fold, and the female parasite appears to prefer the middle segments for oviposition.

Although *G. gallicola* exclusively attacks larvae, it prefers to deposit eggs along the host's dorsum. This habit is consistent with studies of *Parasierola nigrifemur* (Ashmead) and all literature statements regarding egg deposition by *Parasierola* (Avasthy and Chaudhary *1966*; Bridwell *1919*; Busck *1917*; Ramachandra Rao and Cherian *1928*). More distantly related bethylids may also deposit eggs longitudinally, but they prefer a different site (cf. Powell *1938*; Rilett *1949*; van Emden *1931*). *Laelius anthrenivorus* Trani, for instance, deposits eggs along the longitudinal axis of its host, *Anthrenus verbasci* (Linnaeus), but it prefers the abdominal sternites (Vance and Parker *1932*).

Larval and Pupal Development

Stadium duration and the number of larval instars are difficult to determine for *G. gallicola* and have not been conclusively established for any bethylid. By measuring exuvial spiracle diameters van Emden (*1931*) concluded that *Cephalonomia quadridentata* has five instars. Nickels and Pinkney[2] implied that *Parasierola cellularis* var. *punctaticeps* has only three instars, and Yamada (*1955*) indicated that *Allepyris micronevrus* Kieffer has only two larval instars on its primary host, *Anthrenus verbasci*. Such a variety of instar numbers seems unlikely, especially when all bethylid larvae are similar in morphology and behavior. *G. gallicola* has at least three instars and possibly a fourth.

The construction and shape of bethylid cocoons seem remarkably similar, but coloration varies among species. Although cocoons of *G. gallicola* and the Ethiopian *Goniozus* are white, *G. marasmi*, *G. indicus*, and *G. japonicus* have brown cocoons (Iwata *1949*). *Parasierola cellularis* has a white cocoon on the shuckworm and a brown cocoon on the nut casebearer (Nickels et al. *1950*). *Parasierola nigrifemur* produces a white cocoon on *Pectinophora gossypiella* and *Phthorimaea operculella*. A literature survey indicates that all other species of *Parasierola* produce white cocoons.

The sequence in which pupal body parts become pigmented in

[2] NICKELS, C. B., and PINKNEY, C. C. PERISIEROLA CELLULARIS VAR. PUNCTATICEPS (KIEFFER) A PARASITE OF THE PECAN NUT CASEBEARER. 29 pp. [Unpublished. Copy on file Univ. Calif., Riverside.] [1930–40.]

G. gallicola was invariant. Although pigmentation of other bethylids has not been carefully analyzed, information concerning the sequence in which body parts become colored may prove useful in determining subfamilial and generic phylogeny. For instance, Rilett (*1949*) found that *Cephalonomia waterstoni* Gahan became pigmented on the gaster first, with coloration proceeding cephalad. Studies on the Ethiopian *Goniozus* sp. and Colombian *Parasierola nigrifemur* revealed that both species were pigmented similarly to *G. gallicola*.

Mating and Sex Ratio

Protandrous males mating with females inside the cocoons have been observed in *G. claripennis* (Voukassovitch *1924*) and in this study of *G. gallicola*. In both species the copulatory stance is venter to venter inside the cocoon, but males mount the females after female emergence. This change in copulatory approach may be attributed to females inside the cocoon being teneral, and mounting by the male may result in damage to the wings or other body appendages.

Multiple mating by pairs of bethylids has been reported for *Allepyris microneurus* (Yamada *1955*) and in the present study for *G. gallicola*. Experimental evidence in this bulletin suggests that females are exceptionally long lived, and the sperm supply may be depleted. When this occurs, mating with a second male, possibly a son, insures the production of additional females, since *G. gallicola* is arrhenotokous.

Sex ratio phenomena in bethylids have not been critically examined. This study suggests that *G. gallicola* can regulate its sex ratio, since there is a sharp transition in male production for large broods. One hypothesis that might account for the transition in male production is that males can inseminate a limited number of females. Since males emerge first and mate with siblings, selection could operate to produce only enough males to mate successfully with the female progeny of a given brood. In addition to being parsimonious with regard to taxation of a resource, since males are only necessary for genetic recombination and reproduction, such a strategy would seemingly be consistent with the parasite's ability to determine host size and the subsequent deposition of a predicable number of eggs.

Parasite Attack

The manner in which prey is subdued seems similar for most bethylids. All known Lepidoptera parasites attack and paralyze

their prey by injecting the sting in or near the ventral nerve cord. Some variation in the approach of the female has been noted. *Scleroderma chilonellae* Bridwell, a parasite of beetle larvae, stings the host repeatedly with backward thrusts of the sting to the head region, but it does not apparently attach to the host. *G. gallicola* may thrust the sting into the cuticle near the nerve cord several times in rapid succession, but whether more than one injection of venom is necessary for paralysis is uncertain. *G. japonicus* and *G. marasmi* apparently require only one thrust to subdue the host (Venkatraman and Chacko *1961*). Available information suggests *Parasierola* exhibits a wide range of sting thrusts.

Host paralysis by the Ethiopian *Goniozus*. *G. japonicus* (Iwata *1961*), *G. marasmi* (Venkatraman and Chacko *1961*), and *G. claripennis* (Voukassovitch *1924*) is temporary, with the host recovering some locomotion after a few hours. Similar findings have been reported by Taylor (*1933*) for *Goniozus* sp. attacking *Nacoleia octosema* Meyrick, in which the host may also spin a cocoon. In contrast, available information suggests that *Parasierola* spp. immobilize their hosts permanently. Since host paralysis by *G. gallicola* is permanent, this is another biological characteristic indicating that it resembles *Parasierola* more than *Goniozus*.

Finlayson (*1950a*) reported that *Cephalonomia waterstoni* permanently paralyzes *Laemophloeus ferrugineus* (Stephens). However, in an edited reprint of that publication sent to C. P. Clausen, the text reads (*p. 83, lines 16–18*): "Recovery from stinging, as occurs in the hosts of several species of *Goniozus* (e.g., *G. claripennis* Foerst., Voukassovitch 1924), has been observed in *Laemophloeus* [*in very few cases*]."

Prey transport has been seen in *Bethylus* (Chatterjee *1941*; Haliday *1835*; Nielsen *1903*; Richards *1932*), *Epyris* (Bridwell *1917*; Williams *1919*), *Laelius* (Krombein *1955*), *Holepyris*, *Parascleroderma*, and some *Cephalonomia* (Yamada *1955*). This habit has not been recorded for *Goniozus*, but during this study females were occasionally observed attempting to drag paralyzed hosts up the side of the container. This behavioral response persisted for 1 or 2 minutes but was ultimately abandoned. These observations suggest the remnant of a behavioral characteristic found in related taxa and thus a primitive character. The response has not been observed in the Ethiopian *Goniozus*, but perhaps with critical examination of other *Goniozus* species and *Parasierola* this feature will be noticed. It is interesting that Krombein (*1955*) interpreted prey transport by *Laelius trogodermatis*

Ashmead as depending on whether the host was concealed. Whenever this phenomenon was observed for *G. gallicola*, the host was exposed.

Maternal care has been witnessed for *Parasierola nephantidis* by Antony and Kurian (*1960*), for *Bethylus distigma* Motschulsky by Chatterjee (*1941*), for *Prosierola bicarinata* (Brues) by Doutt (*1973*), and by me for *Parasierola nigrifemur*. *G. gallicola* did not display progeny defense, although a female parasite may remain near the parasitized host for several hours following oviposition. Sliding the host around with forceps or picking it up will not induce female aggressiveness. This contrasts sharply to the situation found by Doutt (*1973*) for *P. bicarinata*, which actively defended its host when such objects as a brush and dissecting needle were brought near the parasitized larva. *P. nigrifemur* remains on the paralyzed host for up to 2 days following oviposition, but it leaves the host without defense if disturbed. Doutt (*1973*) postulated that maternal care must lower female fecundity because of the extended time the female spends with each host. He further suggested that maternal care compensates for lower fecundity by reducing immature mortality due to hyperparasitism. *G. gallicola* is exceptionally long lived and lays a large number of eggs. These traits may represent an alternative strategy to that outlined by Doutt for *Prosierola*.

Biological Control Potential

Assessment of *P. gallicola* as a potential agent of biological control is difficult. In southern California feral populations of this parasite attack a noneconomically important species of Lepidoptera. In laboratory studies the parasite does attack serious pests of cotton (*Pectinophora gossypiella*) and potatoes (*Phthorimaea operculella*) and thus may prove of some benefit to biological control. The comparatively long life of adult females and large number of eggs produced per female suggest also that the species may be useful. However, the observed lack of specificity may obviate some of the parasite's potential.

In several biological control programs bethylids have been used. These efforts have resulted in different degrees of success. Venkatraman and Chacko (*1961*) reported that *G. marasmi* parasitizes up to 60 percent of *Marasima trapezalis* (Guenée) populations in India. *Parasierola nephantidis* has been considered an effective parasite of *Nephantis serinopa* Meyrick in India, Burma, and Ceylon (Antony and Kurian *1960*; Dharmaraju *1952*; Jayaratnam *1941*; Kurian and Antony *1961*; Ramachandra Rao and Cherian *1928*). Iwata (*1961*) reported that the host spectrum of

G. japonicus varies seasonally, with the parasite attacking numerous species in the spring but concentrating on only a few species in the fall.

It is reasonable to assume that because *G. gallicola* is endemic to California it would not prove effective in California on endemic pests unless mass reared and released in inundative control programs. In other areas it may act in concert with other parasites and predators to control some lepidopterous pests that live in concealed habitats. Importation of this parasite into other areas for potential control of introduced pests may be desirable.

SUMMARY

The life history, immature stages, and imaginal behavior of *Goniozus gallicola* Fouts are described. This is a primary, gregarious, external parasite of lepidopterous larvae. Laboratory studies suggest that this wasp was not host specific and does not exhibit instar preference. In the field *G. gallicola* has been recovered from *Deoclona yuccasella* Busck. In the laboratory it readily parasitizes *Pectinophora gossypiella* (Saunders), reluctantly parasitizes *Phthorimaea operculella* (Zeller), and does not parasitize *Trichoplusia ni* (Hübner). Immature development and oviposition behavior are similar for *D. yuccasella* and *P. gossypiella*.

Mean feeding time for 84 parasite larvae was 3.6±0.5 days. Protandrous males chew into female cocoons and mate with siblings before emergence. The sex ratio of *G. gallicola* fluctuates with brood size: Broods of 10 or less generally produce only 1 male; larger broods invariably yield more.

Forty-one mated female parasites that were continually provided hosts lived 62.43±8.48 days and deposited 153.78±48.59 eggs. Unmated males and unmated and mated females that were continually provided honey but deprived of hosts lived as long as females provided hosts. Males that mated with several females died less than 8 days after emergence.

The venom used by female parasites to subdue their hosts appears localized in its effectiveness. Only host larvae stung at or near the ventral nerve cord immediately caudad to the gula are paralyzed.

G. gallicola prefers to deposit eggs on segments 6–9 of the host's dorsum and seldom on its lateral and ventral aspects. A linear relationship between size of the host and number of parasite eggs deposited was established: Small hosts receive fewer

eggs than larger hosts provided the female parasite has been mated. This relationship does not hold if parasites are unmated.

Biologically *G. gallicola* is more nearly related to species of *Parasierola* than to any species of *Goniozus;* morphologically *G. gallicola* is clearly assignable to the genus *Goniozus.*

An assessment of *G. gallicola* as a potential biological control agent is discussed.

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